COMPARISON OF THE INFLUENCE OF TWO EXOTIC COMMUNITIES ON ECOSYSTEM PROCESSES IN THE BERKELEY HILLS

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ABSTRACT

The introduction of exotic plant species can provide insight into the biotic regulation of ecosystem processes. Many coastal California ecosystems have been changed by the introduction of exotic species, two of which are the blue-gum eucalyptus species (*Eucalyptus globulus*) and annual grasses species in the genera *Bromus, Avena* and *Lolium.* In this study, we compared the rates of ecosystem processes such as production and decomposition on sites dominated by these two exotic communities. *Eucalyptus* litter was produced in greater quantity and decomposed more slowly than litter produced in annual grasslands. Consequently, the litter layer in *Eucalyptus* sites was nine times larger than in annual grasslands. These results indicate that, under similar climatic and edaphic conditions, the characteristics of the plant species caused large differences in ecosystem processes.

State factors governing ecosystem processes include climate, parent material, topography, time, and biota (Jenny 1941, 1980). Of these factors, the influence of the biota has received the least attention. The invasion of exotic species provides an opportunity to study the impact of plant species on rates of ecosystem processes such as productivity and nutrient cycling (Vitousek 1990). For example, nitrogen-fixing exotic species can alter nutrient cycling (Vitousek et al. 1987), while other exotic species can alter disturbance regimes (D'Antonio and Vitousek 1992).

It is usually difficult to study biotic effects on ecosystem processes because different communities occupy different positions along environmental gradients. Coastal California provides a unique opportunity to study biotic effects on ecosystem processes because of a wide range of introduced species. Annual grasslands and *Eucalyptus* groves, both widespread exotic communities in California, have very different life-histories and phenologies which may influ-

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ence ecosystem processes. *Eucalyptus globulus* is a long-lived, evergreen tree which is active throughout the year, whereas annual grasses in the genera *Bromus, Avena,* and *Lolium* are annuals which are active only for a small portion of the year (Heady 1977).

The purpose of this study was to determine whether or not these exotic communities exhibit different rates of litter production and decomposition, and if so, to determine to what extent these differences may be attributed to the life form characteristics of the dominant plants. We expected that *Eucalyptus* groves would exhibit larger litter layers than annual grasslands because (1) on an annual basis, *Eucalyptus* trees produce more litter than annual grasses and (2) *Eucalyptus* litter decomposes slower than grass litter.

Study Site and Methods

The study was conducted in Tilden Park near Berkeley, California (Fig. 1). The long-term averages of precipitation and temperature at the site are 47.5 cm and 14.1°C, respectively (WRCC 1993). In 1992–1993, when the study was conducted, annual precipitation was 67.6 cm and mean temperature was 15.9°C (WRCC 1993). Five paired sites of *Eucalyptus* groves and annual grasslands were selected, each of at least 400 m^2 area and between 700–800 ft elevation (Fig. 1). All sites were on west-facing slopes. Two sites were located on soils derived from volcanic parent material, whereas the other three sites were on soils derived from a sandstone conglomerate material (Gordon personal communication).

Aboveground litter production of annual grasses was estimated by weighing standing live biomass inside two 20 cm × 20 cm quadrats placed at random points along a 20 m transect. In all cases, random points along the transect were determined using a random numbers table. Aboveground biomass was clipped at the ground surface at the end of the growing season (mid July 1992) and pooled for the two quadrats. Current year's aboveground biomass was separated, oven-dried for 24 hours at 55°C and weighed.

Aboveground *Eucalyptus* litter production was estimated by weighing recent litter (i.e., leaves, stems, bark, fruit) that fell into two 50 cm × 50 cm litter traps placed at random points along a 20 m transect at each site. At the end of each month, the two samples from each site were pooled, oven-dried for 24 hours at 55°C, and weighed. Litter was collected twice in 1993, at the end of February and May, for a total of 11 months of litter production data.

In each forest and grassland site, the litter layer was sampled in five 20 cm × 20 cm quadrats placed at random points along a 20 m transect. *Eucalyptus* litter was divided into two layers, fresh and duff. Fresh litter included all green or light-brown *Eucalyptus* leaves, stems and bark that were only partially decomposed, whereas the

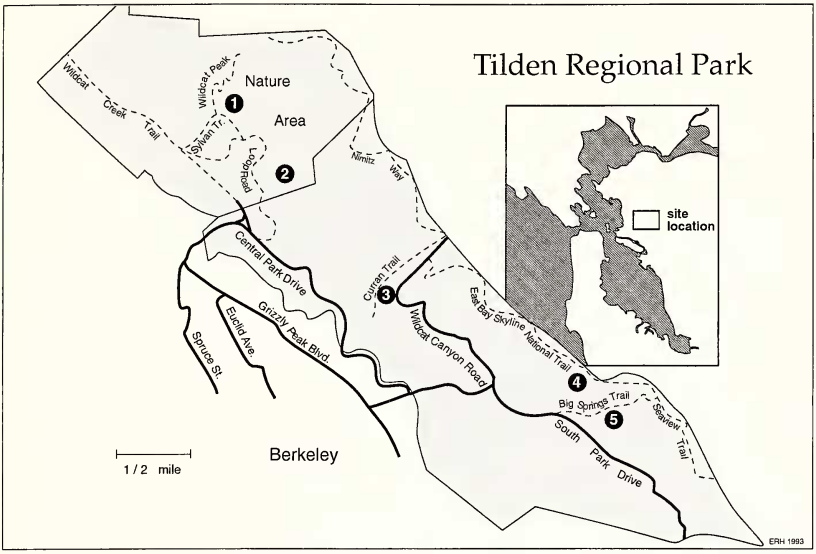

FIG. 1. Map of Tilden Regional Park. Sites 1–5 are indicated by the circled numbers. Source: After EBRPD, 1992. Cartography by Eric R. Havel.

duff layer consisted of more highly decomposed material. There was no duff layer in the grassland. In both cases, litter was collected down to the mineral soil.

To estimate decomposition, 100 grams of fresh litter were collected from one *Eucalyptus* and one grassland site. We estimated the *Eucalyptus* litter to be less than one month old (based on observations of one-month-old litter collected in the litter traps). After removing the dark brown stems from the grass litter, it was assumed that the remaining golden-brown litter was the current year's biomass. Fifteen gram subsamples of each litter type were air dried, and 5 grams were placed in 20 cm × 20 cm nylon mesh bags. Of the other 10 grams in each sample, five grams were oven-dried at 55°C for 24 hours. The dried samples were weighed to determine the actual oven-dry weight of the initial litter. The remaining five grams were used to determine total carbon and nitrogen present in the initial litter. Four litter bags of each litter type were randomly placed along a 20 m transect on each of the 10 sites in early November. In mid-February (after 86 days of decomposition) and late April (after 172 days), two *Eucalyptus* and two annual grass bags from each site were collected. These samples were oven-dried at 55°C for 24 hours, weighed, ground and analyzed for total carbon and nitrogen using a Carbo Erba 1500 C/N analyzer.

All statistical analyses were performed using 2-way ANOVAs in

Systat (Systat 1990). The two independent factors, species and site, and interactions between these two were tested for significance ($P < 0.05$).

Results

Aboveground litter production of *Eucalyptus globulus* stands during the initial six months was 295 g/m^2 (Table 1). There was no consistent pattern of litter production during these six months. In the last five months (Jan–May 1993), the litter mass was 202 g/m^2 for an 11 month total of 497 g/m^2. This amount is more than twice the annual aboveground litter production of grasses, 184 g/m^2 (Table 1). *Eucalyptus* litter layers contained 9 times more material (6.00 kg/m^2) than the annual grasses (0.69 kg/m^2) (Table 1). The *Eucalyptus* litter layer was dominated by the duff layer.

After 86 days of decomposition in the field, mass loss did not differ between species or site (Fig. 2a). However, *Eucalyptus* litter lost N, whereas grass litter gained N (Fig. 3), so that after 86 days, the C/N ratio of *Eucalyptus* litter was significantly higher than that of annual grass litter (Fig. 2b). After 172 days of decomposition, annual grass litter had lost a significantly greater proportion of its initial mass (Fig. 2a) and nitrogen (Fig. 3) than did the *Eucalyptus* litter. *Eucalyptus* litter in the *Eucalyptus* site decomposed faster than *Eucalyptus* litter transplanted into the grassland (Fig. 2a). The C/N ratios of this period were consistent with the mass loss results. The grass C/N, after 172 days, was significantly lower than the *Eucalyptus* C/N, and the C/N of the *Eucalyptus* litter placed on *Eucalyptus* sites was significantly lower than on grass sites (Fig. 2b).

Discussion

The estimate of *Eucalyptus* litter production in this study (497 g/m^2) is lower than other studies of *Eucalyptus* species in wetter environments (700–900 g/m^2, Binkley et al. 1992; 1500 g/m^2, Lugo et al. 1990). The grass litter production reported here (184 g/m^2) is within the range, (78–290 g/m^2) of long-term litter production of annual grasses (Heady 1977). Even though the *Eucalyptus* litter production estimate is low, it is over two times larger than the grass litter production. Because these two communities were under similar climatic and edaphic conditions, this result, as well as the large difference in litter layer mass, suggest that the inherent characteristics of the community dominants may explain differences in litter production. *Eucalyptus* trees contain leaves which are active 12 months of a year, whereas annual grass leaves are active for only 7–8 months of the year (Heady 1977).

TABLE 1. LITTER PRODUCTION AND LITTER LAYER MASSES PRESENT ON *EUCALYPTUS* AND ANNUAL GRASS SITES. Numbers are means of replicate samples (n = 10) and standard errors. Estimates of litter production between Jan–Feb and Mar–May were increased by 10% to account for decomposition in the field (Fig. 2a). Total for *Eucalyptus* litter production and fuel load were significantly larger than those of annual grasses.

Month	*Eucalyptus* litter production (g/m²)	Annual grass litter production (g/m²)	*Eucalyptus* fuel load (kg/m²)	Annual grass fuel load (kg/m²)
July	38 ± 2		duff 5.4 ± 0.5	
August	25 ± 3		fresh 0.6 ± 0.06	0.69 ± 0.05
September	60 ± 8			
October	49 ± 5			
November	35 ± 7			
December	88 ± 9			
Jan–Feb	103 ± 24			
Mar–May	99 ± 15			
Total	497 ± 41	184 ± 25	6.0 ± 0.58	0.69 ± 0.05

As with litter production, litter decomposition was governed by inherent differences between the species, in this case the quality of litter. Because the litter of many *Eucalyptus* species contains large amounts of lignin and resin (O'Connell 1988), we suspect the high initial carbon concentration in the *Eucalyptus* litter (data not shown) resulted from substantial amounts of lignin relative to the grass tissue. Thus, the slower decomposition of *Eucalyptus* litter on both sites seen after 184 days can be explained by the life-form difference.

The results of the second decomposition period showed that *Eucalyptus* litter was prone to decompose faster in the *Eucalyptus* sites than in annual grass sites. Microbes in the *Eucalyptus* groves may be better suited (via natural selection) to consume *Eucalyptus* litter than microbes in the annual grasslands. If so, litter type has a secondary, indirect influence on decomposition via specialization of microbial fauna.

The N dynamics of decaying leaf litter provide insight into feedbacks between species and ecosystem processes. After 86 days of decomposition, *Eucalyptus* litter lost N while annual grass litter immobilized N (Fig. 3). The decreasing N content in *Eucalyptus* litter may have led to higher soil N mineralization rates during this period (McClaugherty et al. 1985). This trend was reversed during the second decomposition interval, where more N was lost in the grass sites than in the *Eucalyptus* sites (Fig. 3). Because the quality of *Eucalyptus* litter after this interval was low compared to the grass litter, we expected the trend of N retention in the *Eucalyptus* litter relative to grass litter to continue and act as a negative feedback

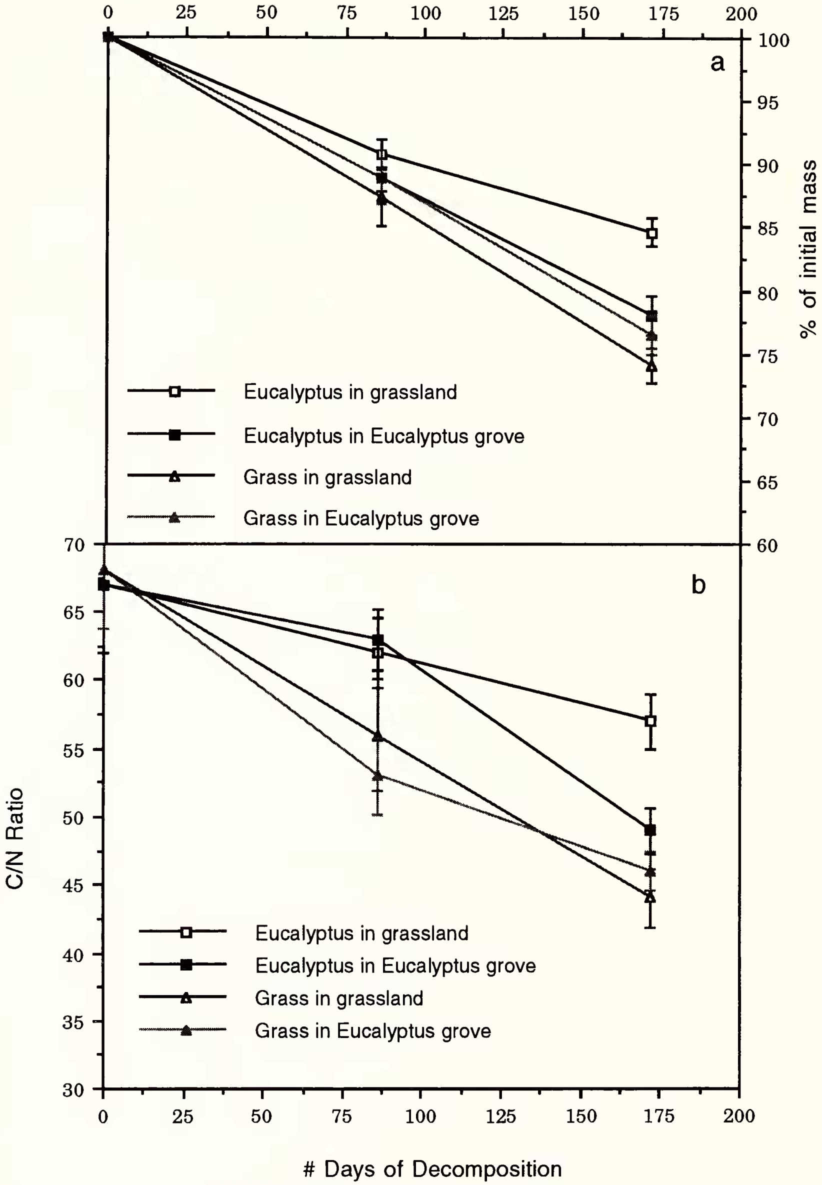

FIG. 2. (a) Percent of initial biomass of litter types placed on *Eucalyptus* and annual grass sites calculated as: (Initial Mass − Final Mass)/Initial Mass·100. Differences between litter types and between *Eucalyptus* litter on each site were significant at 172 days. Vertical bars in (a) and (b) represent standard errors. (b) C:N ratios of litter types placed on *Eucalyptus* and annual grass sites. Differences between litter types were significant at 86 and 172 days and differences between native and transplanted *Eucalyptus* litter were significant at 172 days.

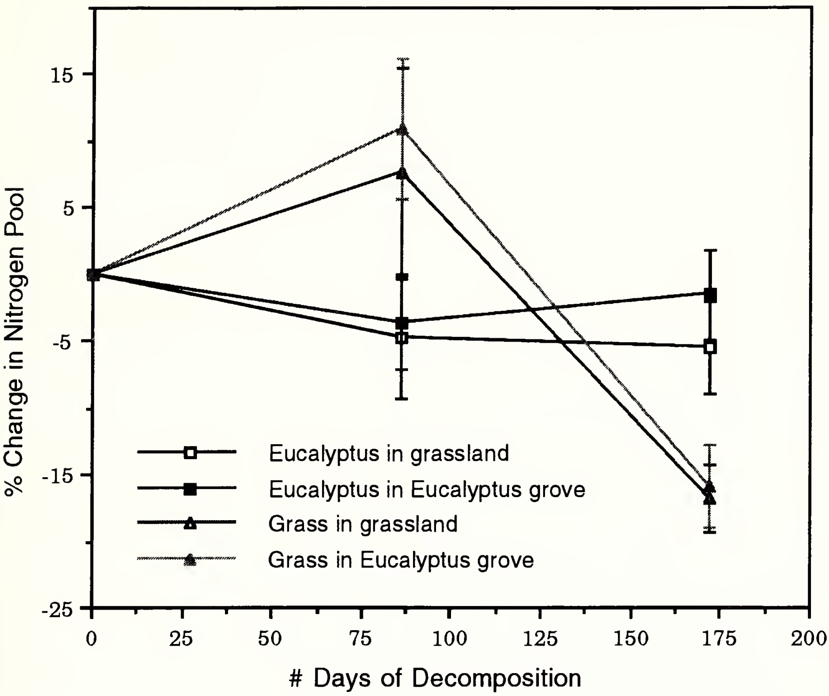

FIG. 3. Percent change in N pool of litter types on both sites calculated as: (grams N of initial litter − grams N final litter)/(grams N of initial litter).

between litter production and N availability. *Eucalyptus* trees may be able to sustain high litter production rates despite slow rates of decomposition and soil N mineralization by exploring deeper layers in the soil profile. The root profiles of *Eucalyptus* trees are much more extensive at deeper depths than those of annual grasses which are typically concentrated in the top 5–10 cm (Jackson et al. 1988). Thus, stands of *Eucalyptus* are sustained by a difference in life-form (i.e., rooting depth) once they establish and alter the N cycling of the site.

One important consequence of exotic species invasions is the alteration of disturbance regimes (Vitousek 1990; D'Antonio and Vitousek 1992). The East Bay fire of October 1991 is a recent example of the many wildfires that plague the coastal hills of California. What role did *Eucalyptus* groves and annual grasslands play in this and other fires? Using computer simulation, Van Wilgen and Richardson (1985) found that exotic shrubs that produced larger litter layers than native shrubs exhibited lower simulated rates of fire spread and intensity due to densely-packed litter layers. They concluded that densely packed litter layers may increase fire hazard only under extreme conditions, such as very dry conditions. These results may apply to this system, in that one community, *Eucalyptus* groves, produced large amounts of densely-packed litter, whereas another, annual grasslands, produced small amounts of litter which is less densely-packed. One consequence of this apparent pattern is that *Eucalyptus* may influence fire intensity whereas annual grasses may influence fire frequency in the California coastal hills.

Acknowledgments

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Literature Cited

Bargali, S. S. and S. P. Singh. 1991. Aspects of productivity and nutrient cycling in an 8 year-old Eucalyptus plantation in a moist plain area adjacent to central Himalaya, India. Canadian Journal of Forest Resources 21:1365–1372.

Binkley, D., K. A. Dunkin, D. DeBell and M. G. Ryan. 1992. Production and nutrient cycling in mixed plantations of *Eucalyptus* and *Albizia* in Hawaii. Forest Science 38:393–407.

D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

East Bay Regional Park District (EBRPD). 1992. Tilden Regional Park. Brochure for EBRPD. Oakland, CA.

Heady, H. F. 1977. Valley grassland. Pp. 491–514 *in* Michael G. Barbour and Jack Major (eds.), Terrestrial Vegetation of California. John Wiley & Sons, Inc., New York.

Jackson, L. E., R. B. Strauss, M. K. Firestone, and J. W. Bartolome. 1988. Plant and soil nitrogen dynamics in a California annual grassland. Plant and Soil 110:9–17.

Jenny, H. 1941. Factors in soil formation; a system of pedology, McGraw-Hill, Inc., New York.

———. 1980. The soil resource: origin and behavior. Springer-Verlag, New York.

Lugo, A. E., E. Cuevas, and M. J. Sanchez. 1990. Nutrients and mass in litter and top soil of ten tropical tree plantations. Plant and Soil 125:263–280.

McClaugherty, C. A., J. Pastor, J. D. Abner, and J. M. Melillo. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66:266–275.

O'Connell, A. M. 1988. Nutrient dynamics in decomposing litter in Karri (*Eucalyptus diversicolor* F. Muell.) forests of south-western Australia. Journal of Ecology 76:1186–1203.

Ornduff, R. 1974. An introduction to California plant life. University of California Press, Berkeley.

Penfold, A. R. and J. C. Willis. 1961. The eucalypts: botany, cultivation, chemistry and utilization. Interscience Publishers, Inc., New York.

Systat. 1990. SYSTAT Version 5.0. SYSTAT Inc. Evanston, Il.

Van Wilgen, B. W. and D. M. Richardson. 1985. The effects of alien shrub invasions on vegetation structure and fire behavior in South African fybos shrublands: a simulation study. Journal of Applied Ecology 22:955–966.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7–13.

———, L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois and P. A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238:802–804.

Western Region Climate Center (WRCC). Oakland, CA. 1993. National Climatic Data Center. North Carolina.

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ANNOUNCEMENT

California Exotic Pest Plant Symposium 1995
October 6–8, 1995
Asilomar Conference Center, Pacific Grove California

The California Exotic Pest Plant Council (CalEPPC) announces the fourth annual symposium dealing with a major environmental threat recently attracting nationwide attention. This is the threat to California's natural ecosystems by invasive non-native plant species introduced from around the world.

In California, and throughout the nation, exotic pest plants pose the greatest single threat to the long term integrity of many natural areas and ecosystems. According to one estimate prepared by the Bureau of Land Management, infestations of exotic pest plants are increasing at the rate of approximately 4600 acres per day on disturbed and undisturbed public lands of the west.

The symposium will bring together experts, land managers, public and non-profit agency staff, field practitioners, and concerned citizens who are developing solutions to this major ecological problem. A prominent theme of this year's symposium will be biocontrol—the intentional introduction of carefully selected predator species to control invasive plants.

The keynote speaker will be Randy Westbrooks who will speak on the current weaknesses of APHIS, and how it could be revamped to do a better job. The program and poster sessions will include presentations on the biology of non-native plant invasions, perspectives on biocontrol, and examples of successful control efforts in California and Australia. There will be ample opportunity for participants to exchange ideas and to become involved in CalEPPC projects and programs. A field trip to local habitat restoration sites will cap the symposium on Sunday morning.

For further information contact Sally Davis, P.O. Box 1045, Cambria, CA 93428-1045. Telephone (805) 927-7187.